Are life-history attributes, morphology, and metabolic rate linked in the African cichlid, *Julidochromis ornatus*?

Honors Research Thesis

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Abstract

Climate warming and hypoxia, two forms of human-induced rapid environmental change (HIREC), hold great potential to negatively affect aquatic ectotherms (e.g., fish) by respectively increasing their metabolic rate and the energy required to acquire oxygen from the water. Such increases in energy demand, in turn, could have fitness consequences by reducing the amount of energy available for growth and reproduction. As a first step towards allowing us to understand how novel forms of HIREC might influence aquatic ectotherms, we sought to quantify linkages among metabolic rate, morphology, and reproductive life history under unstressed conditions in *Julidochromis ornatus*, which is a small-bodied fish endemic to, but widely distributed within, Lake Tanganyika (East Africa). In a controlled laboratory setting, we used intermittent-flow respirometry to measure the standard metabolic rate of *J. ornatus* individuals (n=48 breeding pairs, each with a male and female tested individually). We measured several life-history traits, including the mean duration between reproductive events, batch fecundity (mean eggs per brood), and reproductive rate (mean eggs produced per day). We also took morphological measurements, including individual body mass, total length, and volume. Our analyses showed that many of our traits were strongly correlated, with larger individuals having a lower mass-specific metabolic rate, higher batch fecundity, and longer duration between broods than their smaller counterparts. The findings reported herein will provide important baseline information for an impending long-term experiment that will quantify the impact of climate warming and hypoxia on these attributes in *J. ornatus*.

Introduction

Human-induced rapid environmental change (HIREC; Sih, 2011; Sih et al., 2011) is threatening global biodiversity by exposing individuals to environmental conditions that are evolutionarily novel to their respective lineages (Palumbi, 2001; Sih, 2011; Sih et al., 2011; Vitousek et al., 1997). The survival of plant and animal populations, and ultimately species, faced with evolutionarily-novel HIREC (e.g., climate-induced water warming, pollution-induced reductions in dissolved oxygen availability) will depend largely on the existing phenotypic variation within given populations and the capacity for phenotypic plasticity to change within the individuals composing those populations (Charmantier et al., 2008; Schlaepfer et al., 2002; Sih et al., 2012; Sol and Lefebvre, 2000). Many forms of HIREC are expected to influence organisms by altering availability of energy, which is considered the common currency among all organisms (Wikelski and Ricklefs, 2001). For example, water warming associated with climate change and low dissolved oxygen availability (i.e., hypoxia that leads to "dead zone" formation in aquatic ecosystems) associated with nutrient pollution (eutrophication) are expected to negatively influence the energy budget of aquatic animals by increasing their metabolism and by making it more difficult for them to extract required oxygen from the surrounding water to carry out basic life functions (Pörtner et al., 2005; see below). Thus, the ability to understand the impacts of HIREC on individual energy budgets (e.g., rates of metabolism, growth, and reproduction) and how different pieces of the energy budget (consumption, respiration, SDA, egestion, excretion; Beauchamp et al., 1989) are related is crucial to predicting how individuals, populations, and species will cope with a changing environment (Pörtner et al., 2005; Wieser and Medgyesy, 1991).

While ambient temperature has been shown to directly affect energy metabolism in many taxa (Gillooly et al., 2001), it is extremely important in ectothermic organisms whose body temperatures are directly determined by the ambient environment (Hawkins, 1995). In particular, energy budgets of aquatic ectotherms (e.g., fish) are greatly influenced by water temperature. Increasing water temperature has been shown to lead to reduced size (somatic growth; Daufresne et al., 2009) and reproduction (spawning frequency; Pankhurst and Munday, 2011) by increasing metabolic rate (Pörtner, 2001). As a result of the expected increase in metabolic demand due to water warming, an organism's fitness would be expected to decline unless some compensatory mechanism existed to offset this increased need for energy. One such mechanism might include phenotypic change such as a change in physiology (e.g., reduced metabolic rate). Another mechanism might include behavioral change such as an increase in foraging behavior to potentially offset this increased metabolic demand.

Other forms of HIREC hold great potential to affect aquatic ectotherms, including altered nutrient cycling, chemical pollution, invasive species, habitat destruction, overexploitation, and hypoxia (Justić et al., 1996; Mulholland et al., 1997; Noyes et al., 2009; Rahel and Olden, 2008; Sokolova and Lannig, 2008). In particular, hypoxia (dissolved oxygen concentrations $\leq$ 3 mg/L; Ritter and Montagna, 1999), which is a growing problem in freshwater and coastal marine ecosystems worldwide (Diaz and Rosenberg, 2008), holds great potential to negatively affect aquatic organisms. Hypoxia most often occurs in aquatic ecosystems as a result of sediment and nutrient inputs from the watershed that stimulate excessive algal production, and in turn, increase bacterial respiration in bottom sediments (Arnell, 1999; Larkin and Slaney, 1997; Tucker and Slingerland, 1997). Climate warming only further exacerbates hypoxia ("dead zone") formation by reducing availability of dissolved oxygen in the water (Pörtner et al., 2005). Because all

aquatic metazoans require oxygen to fuel aerobic metabolism and other physiological processes, reduced dissolved oxygen availability would be expected to negatively influence aquatic organisms by making it more energetically costly to extract sufficient oxygen from the ambient water. Thus, in hypoxic conditions, organisms that are able to decrease energy use by adjusting their phenotype (e.g., metabolic rate) may not experience as drastic of a reduction in reproductive success as individuals with less phenotypic plasticity.

While climate warming and hypoxia have thus far been discussed independently, both stressors can occur together in nature. For example, during the past century, Lake Tanganyika (the largest member of the East African Rift Lakes and second largest lake in the world) has become warmer, more strongly stratified, less productive, and is now experiencing hypoxia (Dettman et al., 2005; O'Reilly et al., 2003; Tierney et al., 2010; Verburg et al., 2003), with these changes being attributed to anthropogenic climate change (O'Reilly et al., 2003; Tierney et al., 2010) and increased sediment runoff (Dettman et al., 2005). In fact, Lake Tanganyika, which historically has had a stable temperature regime, owing to its large size and tropical climate, is currently experiencing the fastest rate of surface-temperature warming in recorded history (since AD 500). Further, this warming trend is expected to continue into the next century (Tierney et al., 2010). Likewise, an increasing number of instances of localized hypoxia have been observed in Lake Tanganyika due to increasing human population growth in its watershed (Dettman et al., 2005). Similar increases in hypoxia and temperature have been documented in other large ecosystems of the world, including Lake Erie (Hawley et al., 2006; Jones et al., 2006), Chesapeake Bay (Hagy et al., 2004; Najjar et al., 2010), and the northern Gulf of Mexico (Bianchi et al., 2010; Justić et al., 2005).

The combination of increasing temperature and hypoxia, as well as the fact that in some ecosystems (e.g., Lake Tanganyika) these stressors are entirely novel, calls into question the ability of species to persist in the face of continued HIREC. Thus, a fuller understanding of how HIREC will impact these ecosystems and their unique species assemblages is essential. This understanding is especially important when considering that these species can provide important ecosystem services (e.g., food) and also potentially can influence interactions in the broader food web (Duffy, 2003) and ecosystem stability (Tilman et al., 2006). Before we can develop this understanding, however, a relationship must be established between three phenotypic characteristics shown to vary individually under the effects of climate change: morphology, physiology, and life history.

Previous research has begun to fill this information gap. In the case of teleosts, the prevailing evidence indicates that standard metabolic rate decreases with decreasing dissolved oxygen concentration (Crocker and Cech, 1997; Muusze et al., 1998; Schurmann and Steffensen, 1997) but increases with increasing water temperature (Clarke and Johnson, 1999; Crocker and Cech, 1997; Schurmann and Steffensen, 1997; Zweifel et al., 2012). Somatic growth (and, therefore, adult body size) has been shown to generally decrease with increased water temperature, given an inability to compensate (e.g., through increased nutrient uptake) for increased metabolic demands (Neuheimer et al., 2011). Somatic growth has been shown to increase, decrease, or remain the same in the presence of hypoxia (i.e., hypoxia's effects were species-specific; Nilsson and Östlund-Nilsson, 2008). By contrast, reproduction was shown to decrease with hypoxia (Landry et al., 2007), as well as increased temperature (Pankhurst and Munday, 2011).

The predictable relationships that have been observed among morphology, physiology, and reproduction have been described as life-history syndromes (Ferretti et al., 2005; Roff and Fairbairn, 2007). For example, organisms have been placed along a slow-fast life-history continuum (Jones et al., 2008), which explains general relationships between reproduction and morphology (e.g., high reproductive rate, or eggs produced per day, is typically associated with a large body size; Blueweiss et al., 1978). More recently, the pace-of-life syndrome (POLS) was proposed, which included consideration of physiological traits in the slow-fast pace of life continuum (Martin et al., 2006; Ricklefs and Wikelski, 2002; Wikelski et al., 2003). For example, individuals with a slow pace of life generally have a lower reproductive rate, a lower metabolism, a lower growth rate (smaller size-at-age), and a longer lifespan, whereas individuals with a fast pace of life generally have a higher reproductive rate, a higher total metabolism, a faster growth rate (larger size-at-age), and a shorter lifespan (Réale et al., 2010; Wiersma et al., 2012).

Since water temperature and dissolved oxygen concentration can both influence standard metabolic rate, somatic growth, and reproduction, all of which have been shown to be critical components of the energy budget in teleosts (Dabrowski, 1985; Rubin and Dores, 1994), we were interested in quantifying linkages among these traits under normal, unstressed conditions. This baseline information then could be used to inform a future planned investigation that would vary temperature and dissolved oxygen levels in the laboratory (R. Brodnik, I. Hamilton, and S. Ludsin, personal communication). In this context, we explored if the relationships among reproductive life history, morphology, and physiology found at the interspecies and interpopulation level in other studies (on which most POLS research focuses) were expressed at the *intrapopulation* level as well.

Towards this end, we sought to explore how standard metabolic rate, which is defined as the metabolic rate of a completely nonmoving animal in a post-absorptive nutritional state (Beck and Groff, 1995), morphological characteristics, and reproductive life-history traits are related in the Lake Tanganyika cichlid, *Julidochromis ornatus*. We hypothesized that (1) total standard metabolic rate would increase, whereas mass-specific metabolic rate would decrease, with increasing body mass, (2) life-history traits such as fecundity and reproductive rate (determined by brood size and inter-brood duration) would increase with female body mass, and (3) females with a lower mass-specific metabolic rate would have a greater fecundity than females with a higher mass-specific metabolic rate.

Methods

Study System

J. ornatus is a small substrate-brooding cichlid endemic to Lake Tanganyika (Awata et al., 2005; Awata and Kohda, 2004). Populations of *J. ornatus* inhabit rocky shorelines in both the southern and northern portions of the lake. *J. ornatus* is mostly monogamous (including in our laboratory population), but large individuals of both sexes often have multiple mates at different nests, which consist of rock crevices (Awata et al., 2005; Awata and Kohda, 2004). *J. ornatus* is a good representative Lake Tanganyikan species because it is found throughout the entire lake, suggesting that it is well adapted to historical conditions. In addition, it is ecologically similar to many other cichlid fishes in this ecosystem (Awata et al., 2005).

Experimental Set-up

We used a common cohort (same age and parentage, with previous environmental conditions known) of *J. ornatus*, which was two generations removed from Lake Tanganyika.

This study population consisted of 48 breeding pairs, which were maintained at The Ohio State University's Aquatic Ecology Laboratory. Each breeding pair was individually housed in a 57 L aquarium that contained a breeding cave (Fig. 1a) made of slate tiles that facilitates natural territorial and reproductive behavior in *J. ornatus*. These tanks were equally divided among four independent recirculating systems (Fig. 1b) that were maintained at the same water temperature (25°C) and dissolved oxygen concentration (90% saturation). Each of our 48 breeding pairs had produced at least three broods. All breeding pairs were fed standard cichlid pellets at a standard ration (2 pellets per day). Water temperature, dissolved oxygen, ammonia, and pH were monitored daily, with conditions remaining fairly constant during the entire period of captivity at Ohio State.

Life History

All tanks were observed daily for the presence of eggs, with eggs being counted when found. We used these data to determine mean brood size (i.e., number of eggs per reproductive brood), median brood frequency (i.e., number of days between first the first sign of eggs between each brood), and number of eggs produced per day (i.e., reproductive rate). These three reproductive traits were used to characterize the reproductive life-history strategy of each breeding female.

Body Size and Metabolism

We determined the standard metabolic rate of all breeding adults through measurements of dissolved oxygen consumption during respirometry trials of known duration. Both individuals within a breeding pair were tested simultaneously, but in two independent respirometers.

Respirometry trials were conducted on breeding pairs within 5 to 11 d after the pair produced a brood. This window of time post-reproduction was chosen to minimize the impact of the reproductive cycle on metabolic rates. To minimize potential error in oxygen consumption measurements due to specific dynamic action (metabolism of food in the gut), fish were fasted for at least 24 hours prior to each trial. Fish also were allowed to acclimate in the water bath for at least 20 min prior to being placed into the respirometry chamber.

Oxygen consumption was measured with a gravity-fed intermittent-flow respirometer (Steffensen 1989). The respirometer (Fig. 2) consisted of one recirculation pump, a 0.15 L cylindrical glass chamber, and an optical dissolved oxygen probe (Vernier Software and Technology) connected to a laptop computer that recorded dissolved oxygen concentration within the system every 6 s. The recirculation pump ran constantly to circulate and mix the water in the system, thus ensuring an equal oxygen concentration within the system. A gravity-fed flush tank intermittently replaced the water in the system with oxygenated water. This process created a repeating cycle consisting of discrete recirculation and flushing phases.

During the recirculation phase, the recirculation pump ran and the fish in the respirometry chamber consumed the oxygen in the closed system. During the flushing phase, a valve connecting the gravity-fed flush tank to the respirometry system via an inlet hose was opened, which allowed new, oxygen-saturated water to enter the system. Simultaneously, a valve at the end of a gravity-fed outlet hose was opened to allow deoxygenated water to exit the system. The dissolved oxygen concentration in the system was then restored to the level of dissolved oxygen in the breeding tank from which the fish was removed.

Each trial consisted of a 20 min “blank” run in which the recirculation pump and dissolved oxygen meter were running but the test chamber was empty. This blank run allowed

us to quantify background oxygen depletion. Following the blank run, three additional runs were conducted, with a fish in the respirometry chamber. Each of these runs lasted up to 30 min, or until the oxygen concentration reached 5 mg/L to ensure our test subjects did not experience hypoxia-induced stress (initial DO concentrations around 8 mg/L). All trials were conducted with the respirometer submerged in a temperature-controlled bath that maintained both water temperature and dissolved oxygen concentrations equivalent to the conditions of the system from which the fish was removed. The gravity-fed flush tank also maintained water temperature and dissolved oxygen concentrations equivalent to the conditions of the system from which the fish was removed. Water flow through the respirometer was low enough that individuals did not need to swim against a current, which would deplete dissolved oxygen faster (Boisclair and Sirois, 1993), but also fast enough that water remained mixed in the system. Each trial was videotaped with a digital camera so that we could eventually quantify caudal fin beats and opercular beats, which could serve as proxies for activity level in the chamber.

After each fish was removed from the respirometer, we recorded its wet mass (nearest 0.1 g), total volume (nearest 0.1 mL), and total length (nearest 1 mm), using standard laboratory techniques, before placing it into its original home tank. The rate of oxygen depletion during each recirculation phase was calculated as the slope of a least-squares regression line between standardized dissolved oxygen concentration (mg of oxygen / L of water) and time (day). Mass-specific standard metabolic rate (mg of oxygen consumed / L of water / g of fish mass / d) was quantified by calculating the total oxygen consumed during the final trial (after accounting for oxygen consumed by the system during the blank run) divided by the wet mass of the fish divided by the time of the final run. All of the test protocols described above have been approved by the IACUC (protocol # 2012A00000112 under PI Stuart Ludsin).

Data Analysis

Pearson's *r* was used to quantify relationships among the physiological (total standard metabolic rate and mass-specific metabolic rate), morphological (mass), and reproductive (reproductive rate, average fecundity, mass-specific average fecundity, and median inter-brood duration) traits. Correlations with a p-value of less than 0.05 were considered significant. Herein, only female data were analyzed due to the established strong relationship between female size and fecundity in fish.

Results

Strong relationships were found among body morphology, physiology, and reproductive life history. For the morphology – physiology relationship, female body mass was positively correlated with total standard metabolic rate ($r = 0.76$, $p < 0.0001$, Fig. 3a) and negatively correlated with mass-specific standard metabolic rate ($r = -0.34$, $p = 0.02$, Fig. 3b). The morphology – life history linkage was exposed by a positive correlation between female body mass and reproductive rate ($r = 0.40$, $p = 0.004$, Fig. 3c), a positive correlation between female body mass and inter-brood duration ($r = 0.36$, $p = 0.01$, Fig. 3d), and a positive correlation between female body mass and average fecundity ($r = 0.69$, $p < 0.0001$, Fig. 3e). A relationship between physiology and life history also was found, as evidenced by a positive correlation between average fecundity and total standard metabolic rate ($r = 0.69$, $p < 0.0001$, Fig. 3f) and a positive correlation between mass-specific average fecundity and mass-specific standard metabolic rate ($r = 0.39$, $p = 0.01$, Fig. 3g).

Discussion

In a controlled, unstressful environment, we found strong linkages among life history, morphology, and physiology in *Julidochromis ornatus*. Similar to other aquatic and terrestrial organisms (e.g., Robinson et al., 1983), standard metabolic rate and mass-specific standard metabolic rate respectively increased and decreased with increasing body size. These results indicate that, although large individuals require more total energy to persist, they use less energy per unit body mass than smaller individuals. We also found that larger females produced broods less frequently and had higher average brood fecundities than smaller females. Correcting for mass, we also found that average fecundity increased with increasing metabolic rate. In other words, females that have higher fecundity also require more total energy than those that have lower fecundity.

These relationships are consistent with the POLS hypothesis (Réale et al., 2010) on an *intrapopulation* level, which is noteworthy because most POLS studies are conducted across populations or species. We found that within our population, variation existed in the expression of morphological, physiological, and reproductive life-history traits. We also found that individuals expressed these traits in suites that varied along a slow-fast pace of life continuum. Indeed, previous research has shown that variation in reproductive rate (Careau et al., 2009), body size (Wiersma et al., 2012), and metabolism (Wiersma et al., 2007) are associated with the pace of life continuum. Some individuals in our population had a lower reproductive rate, a smaller size-at-age, and a slower metabolism (a slow pace of life), whereas others had a higher reproductive rate, a larger size-at-age, and a faster metabolism (a fast pace of life). We know that the individuals in the study were from the same reproductive cohort, thus size can be a used as a proxy for growth rate (size-at-age).

Because large females had higher metabolic and reproductive efficiency per unit body mass (lower mass-specific metabolic rate and mass-specific fecundity) than smaller females while producing more eggs in the same period of time (higher reproductive rate), large size appears advantageous when energy is not limiting. Therefore, under circumstances in which a large body size can be maintained without compromising other traits (i.e., energy is not a limiting factor), larger females may have greater lifetime fitness than smaller females, assuming equal (or at least not drastically different) lifespans. However, under conditions that impose metabolic hardships (e.g., supra-optimal temperatures, hypoxia; Clarke et al., 1999; Herbert and Steffensen, 2005), reproductive output of larger females may be more negatively affected than smaller females. For instance, if lifespans are severely reduced or the time to reach maturity increases as a result of the stress induced by climate warming or hypoxia, smaller females may have a fitness advantage over large females (larger individuals generally have longer lifespans and mature less rapidly according to POLS; Ricklefs and Wikelski, 2002). Also, if the number of hypoxic events and temperature increase, fish will have to put more energy into metabolism and larger females may be unable to maintain a large body size without a reduction in reproductive output (Pörtner and Knust, 2007).

Study Limitations

While we are encouraged by the strong relationships among morphology, metabolic rate, and reproductive life history, our study is limited in several ways. Because physiological and morphological data were collected for each individual only once, we must assume that our relationships will remain constant over time. This assumption may not be a reasonable given that the relationships among growth, metabolism, and fecundity can change with age (Blueweiss

et al., 1978, Robinson et al., 1983, Chen et al., 1992). Additionally, longer respirometry trials (with longer acclimation times than 20 min) may provide more accurate standard metabolism data, as our fish may not have had enough time to acclimate fully to the system. For example, Fisher (2000) performed 2 d trials on two benthic fishes (burbot *Lota lota* and stone loach *Barbatula barbatula*) and found that the fish did not show normal behavior and respiration rates until 3-4 h after being placed in the respirometry chamber.

Conclusions

Our study serves as an initial step towards understanding the impact of HIREC on environmentally stable systems. Under unstressful conditions, small and large *J. ornatus* females appear to use different reproductive strategies. Large females produce large broods infrequently, whereas small females produce small broods frequently. Under stressful conditions imposed by climate warming or hypoxia, in which energy limitations likely will emerge, fitness of large females might be reduced more than small females. Such a fitness reduction could potentially occur in large females if adult longevity is reduced, which in turn reduces the number of broods produced in a female's lifetime (owing to high inter-brood durations in large females). Large individuals have been shown to be less tolerant to hypoxia than small individuals in some species (e.g., yellow perch *Perca flavescens*; Robb and Abrahams, 2003; largemouth bass *Micropterus salmoides*; Burleson et al., 2001); however, the opposite has been shown in others (e.g., Oscar cichlid *Astronotus ocellatus*; Almeida-Val et al., 2000).

Future Work

We encourage continued research into how reproductive life history, morphology, and physiology co-vary over an individual's lifetime. The POLS hypothesis suggests that across

populations or species, individuals that grow quickly and produce more offspring should also have a shorter lifespan (Réale et al., 2010). It is of direct interest to determine if the lifespan portion of the hypothesis holds true between individuals from the same population as well. Another interesting aspect to explore is how variation in behavior or personality (i.e., behavioral differences that are consistent over time and/or across situations; Réale et al., 2007) between individuals is correlated to physiology, morphology, and life history (Réale et al., 2010). For example, exploration (Dingemanse et al., 2003; Dingemanse and de Goede, 2004), boldness (Johnson and Sih, 2007), activity (Verbeek et al., 1994; Dingemanse et al., 2002), and stress response (Carere and van Oers, 2004) have been shown to correlate with metabolism, suggesting physiology is a driver of personality.

We also encourage research that contrasts the short- versus long-term, as well as independent versus interactive, impacts of HIREC on aquatic ectotherms (e.g., *J. ornatus*), which have no known exposure to these stressors in their recent evolutionary history. Many studies have looked at the immediate (short-term) effects of hypoxia, but few have explored its long-term (sublethal) effects (Rose et al., 2009) and none has examined the combined (and possibly interactive) effects of long-term hypoxia along with increased temperature. Ambient water temperature and dissolved oxygen, when acting independently, appear to have opposing influences on metabolic rate (Clarke and Johnson, 1999; Crocker and Cech, 1997; Muusze *et al.*, 1998; Schurmann and Steffensen, 1997; Zweifel *et al.*, 2012). Therefore, the critical knowledge gap regarding how standard metabolic rate changes in both the short- and long-term, when fish are exposed to all combinations of dissolved oxygen and water temperature (all combinations are realistic scenarios in the case of Tanganyikan cichlids), deserves further investigation.

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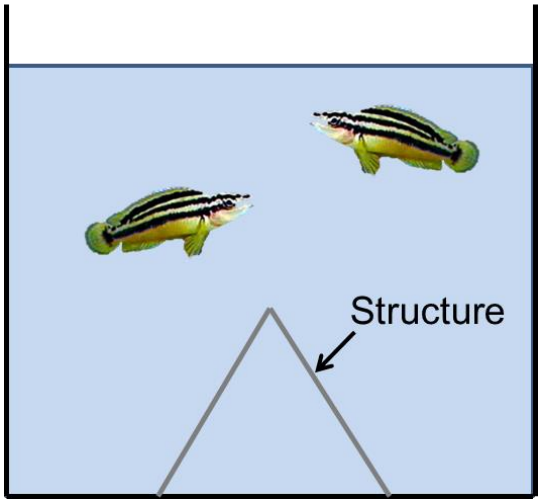
Figures

Figure 1. Diagram of a) the breeding structure inside the home tank of a breeding pair of *Julidochromis ornatus* and photograph of b) 2 of our 4 independent recirculating systems that housed breeding pairs of *J. ornatus*.

a)



b)

Figure 2. We used gravity-fed intermittent-flow respirometry to quantify the standard metabolic rate of adult females. A continuously running recirculating pump brought water to the dissolved oxygen (DO) sensor port and ensured that DO was uniform throughout the system. Before each run during a trial, the gravity-fed flush-in would be opened to allow new, oxygen-saturated water to enter the system and the gravity-fed flush-out would be opened to allow deoxygenated water to exit the system.

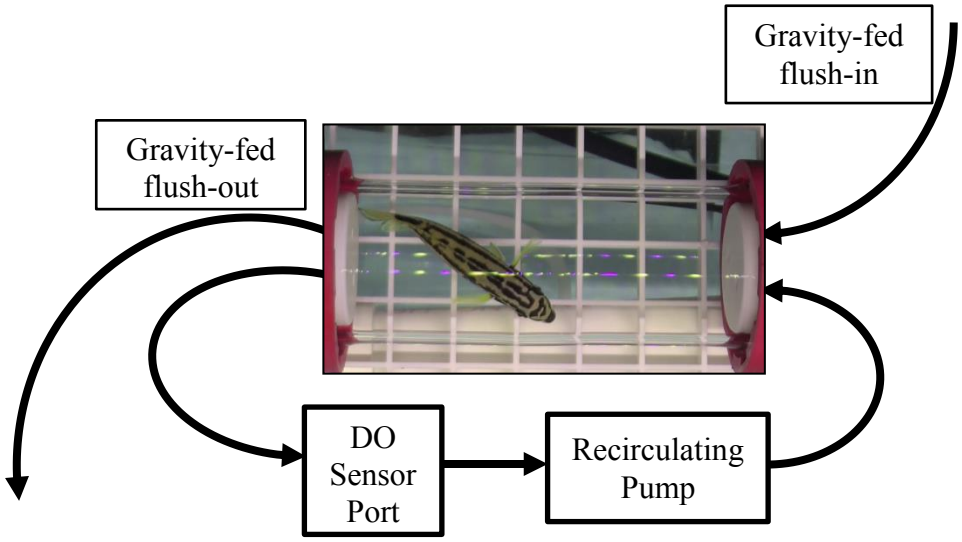
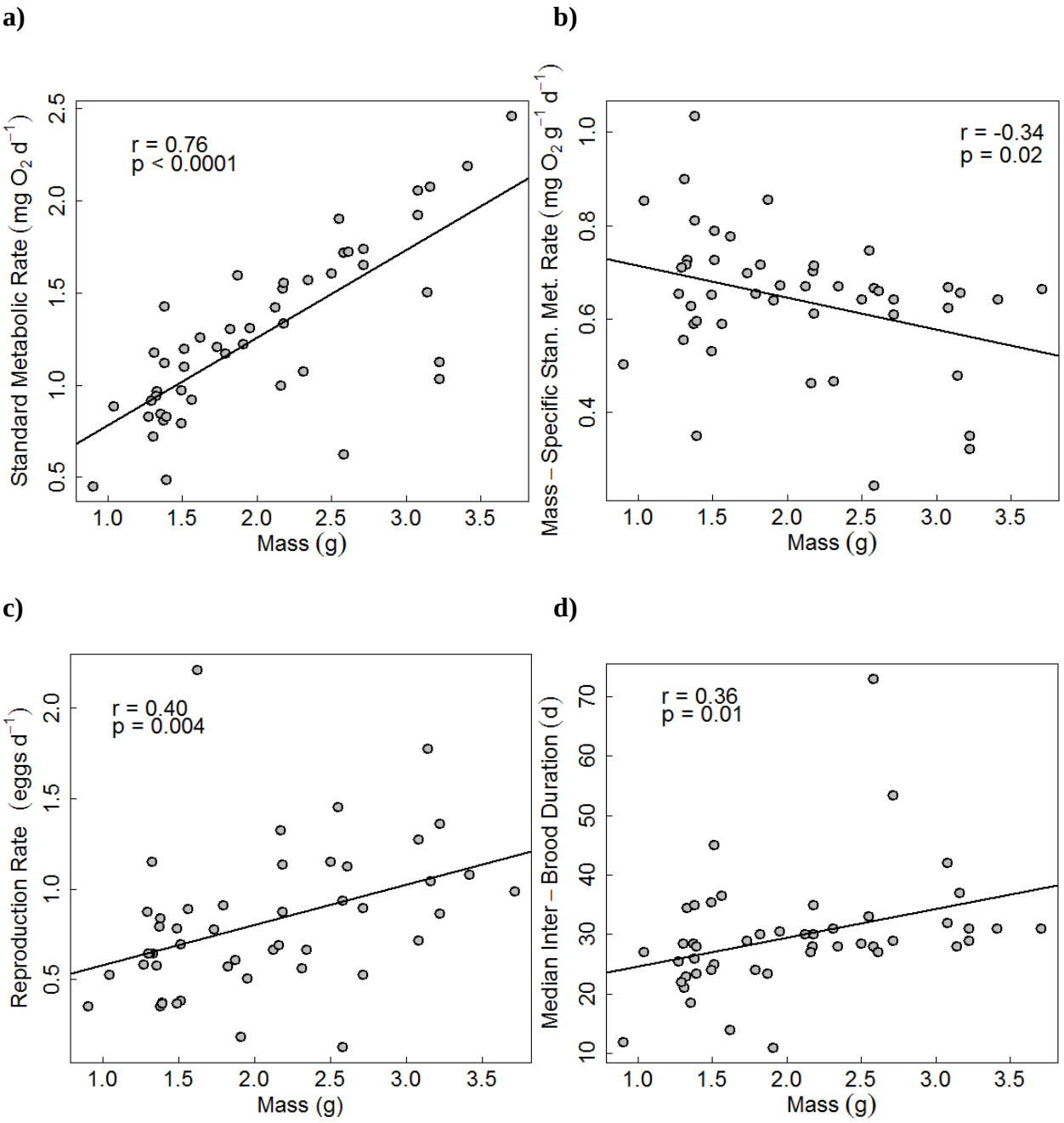
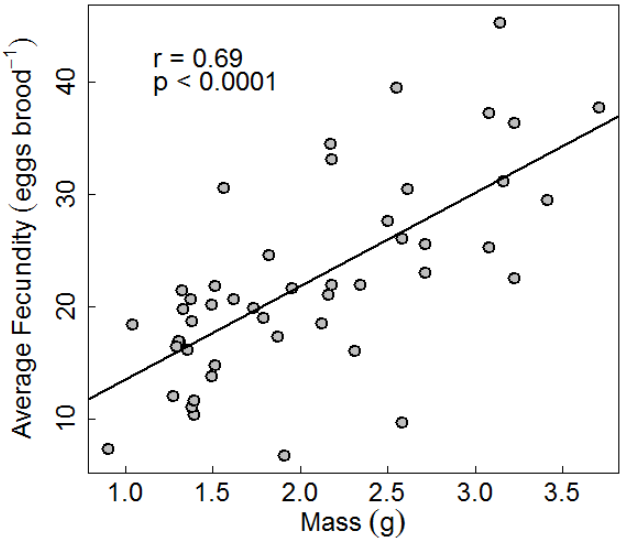


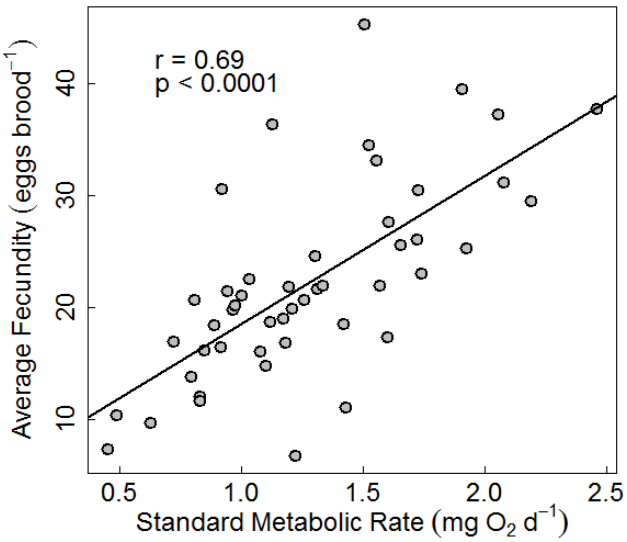
Figure 3. Correlations between individual a) body mass and standard metabolic rate, b) body mass and mass-specific standard metabolic rate, c) reproductive rate and body mass, d) body mass and median inter-brood duration, e) body mass and average fecundity, f) total standard metabolic rate and average fecundity, and g) mass-specific average fecundity and mass-specific standard metabolic rate. Each point represents an individual adult *J. ornatus* female (n = 48).



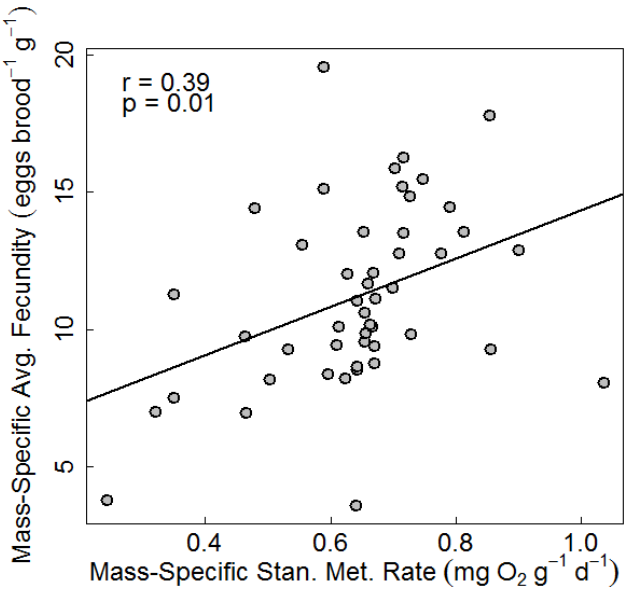
e)


r = 0.69
p < 0.0001
Average Fecundity (eggs brood^{-1})
Mass (g)
10
20
30
40
1.0
1.5
2.0
2.5
3.0
3.5

f)


r = 0.69
p < 0.0001
Average Fecundity (eggs brood^{-1})
Standard Metabolic Rate (mg O_2 d^{-1})
10
20
30
40
0.5
1.0
1.5
2.0
2.5

g)


r = 0.39
p = 0.01
Mass-Specific Avg. Fecundity (eggs brood^{-1} g^{-1})
Mass-Specific Stan. Met. Rate (mg O_2 g^{-1} d^{-1})
5
10
15
20
0.4
0.6
0.8
1.0